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Concept for APODEMUS – a wood mouse population model for pesticide risk assessment

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Abstract

The wood mouse, *Apodemus sylvaticus*, is a small mammal species that occurs across large parts of Europe. The species uses various habitats, has an omnivorous diet and can use pesticide-treated agricultural fields for foraging. Thus, it is one of the focal species in risk assessments of plant protection products (PPPs) in the European Union. However, exposures and effects of PPPs on populations in the field are challenging to assess across different regions and landscapes. Population modelling is suggested as a tool in higher-tier risk assessments, complementing and extending data from field studies. Population models can predict population-level effects from modelled life-cycle processes and individual-level exposure and effects. We present the development of a conceptual model for APODEMUS, a POpulation Dynamical spatially Explicit Model of the wood mOUSe. We used best practices for model development recommended in recent guidance documents by the European Food Safety Authority (EFSA). Thereby, we focus on the ecological model without the explicit representation of exposures and effects of PPPs as the first part of the model development. We conducted a comprehensive literature search and review on wood mouse ecology. The resulting data compilation was used as the basis for the development of the conceptual model. Decisions about processes included in or excluded from the model were taken in collaboration with stakeholders including small mammal experts, risk assessors and regulators, as well as ecological modellers. Beyond the presentation of the conceptual model for APODEMUS, we discuss the importance of stakeholder involvement in the model development process. In addition, we suggest additions to the comprehensive approach to model development for ecological risk assessment (Pop-GUIDE), particularly with respect to risk assessments of small mammals in the European Union. Our study shows how the systematic development of a population model with continued stakeholder support can lead to a transparent tool for higher-tier risk assessments.

Key words: *Apodemus sylvaticus*, conceptual model, pesticide risk assessment, Pop-GUIDE, small mammal, spatially-explicit, stakeholder involvement, transparent modelling decisions

Introduction

The wood mouse, *Apodemus sylvaticus* L., is one of the focal species (European Food Safety Authority 2023) for higher-tier risk assessments of mammals in the European Union. The species occurs across large parts of Europe from Scandinavia to the Mediterranean (Herman et al. 2017) and occupies a wide range of habitats (Healing et al. 1983; e.g. Rogozi et al. 2013), including agricultural landscapes (e.g. Tattersall et al. 2001; Janova and Heroldová 2016). It has been reported to feed on a broad diet whereby seeds can make up a large proportion when available (Green 1979).

In the European Union, marketed or applied plant protection products (PPPs) are required to not adversely affect animal health or the environment (European Parliament and Council 2022). Therefore, regulatory ecological risk assessments (ERAs) evaluate potential impacts of pesticide exposure to, among others, birds and mammals (European Food Safety Authority 2023). Laboratory-based ecotoxicological studies are conducted to meet the data requirements by the European Union. Thereby, standard test species for mammals are the Norway rat (*Rattus norvegicus*) and, less frequently, the house mouse (*Mus musculus*) and the European rabbit (*Oryctolagus cuniculus*). ERAs follow a tiered approach, and in the lower tiers of ERAs, toxicity endpoints derived from these studies are compared to worst-case assumptions about potential exposures that could occur in the field. Thereby, dietary exposure is estimated depending on the type of pesticide application (e.g. spray or seed treatment) and feeding guilds (herbivore, omnivore, insectivore, granivore or frugivore). Potential risks are compared to protection goals, which include the survival of individuals (no visible mortality of individuals) as well as long-term sustainability of populations of potentially vulnerable species in a local agricultural field and its surrounding area (European Food Safety Authority 2023). If an unacceptable risk of exposure-related effects cannot be excluded in lower tiers of an ERA, higher tiers address more realistic scenarios. Field experiments can be conducted to estimate the exposure to and effect on focal species under realistic PPP applications. Higher-tier assessment of risks to small mammals can involve field studies to quantify the proportion of diet the animals obtain from treated areas (PD studies), the proportion of time the animals spend in treated areas (PT studies), and the impacts of exposure on field populations (field effect studies). However, such studies are time- and resource-intensive, and it is difficult to address multiple relevant scenarios for risk assessments, for instance, combinations of crop of interest and region. In addition, environmental factors such as weather and small-scale landscape compositions can introduce variability in study data.

Population models have been suggested as tools in higher-tier risk assessments for birds and mammals (European Food Safety Authority 2023). For the integrated exposure and effect risk assessment, simulation models can predict population-level effects from modelled life history processes and individual-level exposure and effects. In addition, depending on the objective of the risk assessment and available information, population models can represent different population-dynamical aspects, such as intra-specific variability, interactions with the environment or social interactions (Accolla et al. 2021; Raimondo et al. 2021). Spatially-explicit population models are relevant if

exposures are expected to vary due to the spatial behaviour of animals in heterogeneous landscapes. They can be used to estimate exposures and effects in different landscape compositions, including the extension of field studies with additional scenarios and estimating the effectiveness of possible mitigation strategies (Galic et al. 2010; Forbes et al. 2016; Hommen et al. 2016; Accolla et al. 2021; Raimondo et al. 2021). The protection goals of risk assessments can be addressed directly with population models because the occurrence of exposure-induced mortality can be observed, and long-term dynamics of populations can be compared in simulated landscapes with and without exposures (European Food Safety Authority 2023). Thereby, exposures can be simulated explicitly in the landscape, i.e. individual-level exposures depend on the spatial and temporal overlap of individuals with treated fields and/or exposed off-crop areas. Toxicodynamic–toxicokinetic models can be incorporated in population modelling approaches to capture individual-level toxicological effect dynamics of temporally variable exposures. In addition to informing higher-tier risk assessments directly, population models can also be applied to support field study design and site selection as well as address uncertainties in study data (European Food Safety Authority 2023).

The development of a population model appropriate for risk assessments requires multiple steps with considerable time investment. Initially, the scope of a model must be framed (EFSA Panel on Plant Protection Products and their Residues (PPR) 2014; Raimondo et al. 2021) by anticipating the risk assessment use cases and their implications (among others, the pesticide application and landscape setting). Ample communication among stakeholders and model developers facilitates shaping an adequate and acceptable risk assessment tool (Raimondo et al. 2021). Substantial knowledge is required to conceptualise the representation of the focal species' ecology adequately in the context of the model objectives. For well-studied species, data from the scientific literature can be used to inform relevant processes in the model. In case of data gaps, information might be extrapolated from related species, but it can exacerbate model output uncertainty (European Food Safety Authority 2023). Further extrapolations are conducted if the model is used to predict landscape-related population-level pesticide effects from standard species sensitivity measured in laboratory studies (European Food Safety Authority 2023), because effects in field settings may differ from effects observed under controlled laboratory conditions. Exposures are variable in the field (Imholt et al. 2023), and exact exposure levels are hard to estimate. To evaluate the validity of extrapolations and identify limits to model applicability, model predictions should be compared to independent data whenever possible (EFSA Panel on Plant Protection Products and their Residues (PPR) 2014). Such data ideally are derived from field studies that represent relevant risk assessment use cases and should directly address the model endpoints as well as secondary multi-dimensional patterns (Wiegand et al. 2003).

An essential prerequisite for the application of population models in ERA is transparency, such that evaluators can retrace the derivation of predicted risks. It is recommended to provide comprehensive documentation of the information base used to inform the model and how the information was processed (EFSA Panel on Plant Protection Products and their Residues (PPR) 2014). Pop-GUIDE, a guidance for the development, use and interpretation of population modelling for ERA (Raimondo et al. 2021), provides a framework for transparent population

model development. Following Pop-GUIDE assures that decisions taken during model development are transparent and documented, and assumptions underlying the model are made explicit – a step considered important for the regulatory evaluation of models submitted for pesticide risk assessments (Becker et al. 2024). Pop-GUIDE is recommended for the development of bird and mammal population models in European ERA (European Food Safety Authority 2023). It requires the documentation and justification of all decisions that are crucial for the model structure, acceptability and domain of application.

Following Pop-GUIDE, we refer to a conceptual model as a definition of the processes explicitly represented in the model as well as the ones that are excluded due to lack of data or because they were deemed not relevant for the model's purpose. A conceptual model is a descriptive blueprint of a model, and it should be comprehensible without experience in mathematical and computer modelling. In addition, the conceptual model aids communication between stakeholders, specifically experts for the ecotoxicological system and species to be investigated, modellers implementing and testing the model, risk assessors using the model outputs and regulators reviewing them.

In the current paper, we present a conceptual model for wood mouse populations (A POpulation Dynamical spatially Explicit Model of the wood moUSe – APODEMUS). The model is intended as a tool to support higher-tier regulatory assessments of risk from pesticides to wood mice in agricultural landscapes, and therefore, we considered generic aspects of exposure and effects of a pesticide. However, in the current paper, we focused on the ecological part of the conceptual model, i.e. the representation of the wood mouse life history and spatial population dynamics without the explicit consideration of exposures to pesticides and their effects. In the following sections, we describe the development of APODEMUS using the five phases of Pop-GUIDE. We state the model objectives (Phase 1) and outline the conducted literature review (Phase 2). We summarise the stepwise development of the conceptual model (Phase 3). We present the final conceptual model (Phase 4), and we provide an outlook on the model evaluation (Phase 5), an important aspect for the acceptability of effect models in pesticide risk assessments (EFSA Panel on Plant Protection Products and their Residues (PPR) 2014). The conceptual model development, particularly Phase 3, benefited significantly from stakeholder involvement, mainly achieved through a dedicated workshop. We summarise the workshop and discussions. To support future model development, we highlight learnings from the conceptual model development process and provide suggestions for possible extensions of Pop-GUIDE. We compare the conceptual model for APODEMUS with previously introduced models of the wood mouse (Loos et al. 2010; Liu et al. 2014; Wang et al. 2022).

Development of a conceptual model for the wood mouse

Phase 1: Objectives of the wood mouse population model

The conceptual model for APODEMUS was developed for use in the European higher-tier ecological risk assessments of pesticides. The wood mouse was chosen because it is a common species occurring in agricultural landscapes and an important focal species in risk assessments, representing omnivorous

and granivorous small mammals (with an adult body weight around 23 g). The spatially explicit model was developed to represent wood mouse populations in different relevant realistic agricultural landscapes across Europe and capture seasonal and annual population dynamics.

The objectives of APODEMUS are to capture and simulate individual- and population-level exposures to pesticides and their effects on wood mouse populations. Thereby, dietary exposure to pesticides is the only exposure route considered for individual mice in the model as presented in the current paper. Individual exposure is considered explicitly and can vary according to differences in the simulated behaviour of individuals in the spatio-temporal pattern of exposed diet in realistic agricultural landscapes. The model should provide the possibility to address realistic exposure scenarios, including conservative or worst-case assumptions related to likely exposures across habitats and seasons. Thus, the model can represent refinements of exposures compared to lower-tier risk assessments on the individual and population level. Individual-level exposure–effect relationships are represented explicitly, extrapolating from laboratory study data with standard test species (e.g. the Norway rat) to the wood mouse. Thereby, sublethal and lethal effects are considered, depending on individual weight or life stage. Simulated population dynamics extrapolate individual-level effects to the population level. The objectives indicate that a realistic and precise model is required according to Pop-GUIDE (Raimondo et al. 2021) and indicate a spatially explicit and individual-based model (IBM).

Model outputs should be comparable (in terms of entities and units) to data available for the wood mouse from field studies and higher-tier studies conducted for ERAs which include numbers and measurements of individual mice (from traps) across habitats over time. Accordingly, model outputs on the individual and population levels are relevant for model evaluation and application, including individual body weights, population abundance and population structure (age, size and sex composition) over time. Thereby, seasonal variation in populations should be captured by the model along with the distribution of mice across habitats. The model includes multiple stochastic processes which will result in variability in model outputs. The stochasticity is based on the reported variability in represented processes in wood mice. However, this variability may not fully reflect variability in actual wood mouse populations. The model concept and implementation should allow future expansion with exposures and effects with corresponding model outputs such as individual-level exposures and individual- and population-level effects. The precision of the model will allow for comparing simulated untreated controls and treatments to analyse effects.

In summary, the model was developed for the domain of applicability defined by 1) wood mouse populations occurring in a local area (excluding regional meta-population dynamics); 2) agricultural landscapes that can be defined by a set of habitat types; and 3) the interaction of the mice with that landscape, with a focus on habitat use related to potential exposures.

In its first iteration, the model was developed to represent the ecology of wood mouse populations without the consideration of pesticide exposures and effects. To ensure that the model will ultimately be applicable for pesticide risk assessments, general considerations about the inclusion of exposures and effects were included in the conceptual model.

Phase 2: Literature review

For the development of the conceptual model, we conducted a comprehensive literature review with the aim of reflecting the current published knowledge about wood mouse ecology. In addition to informing the conceptual model presented in the current paper, data and information compiled from the literature are useful for model parameterisation, providing a systematic path for the justification of parameterisations used for APODEMUS applied in the context of pesticide risk assessments. A documented systematic literature search is considered essential for effect models in pesticide risk assessments because it makes it possible to evaluate whether all relevant data were considered in a model (EFSA Panel on Plant Protection Products and their Residues (PPR) 2014; Becker et al. 2024).

To fulfil suggested requirements on the information base for regulatory models in European ERA, the review followed recommendations for good modelling practice (EFSA Panel on Plant Protection Products and their Residues (PPR) 2014), Pop-GUIDE (Raimondo et al. 2021), Chapter 4 of "Mechanistic Effect Models in the Environmental Risk Assessment of Chemicals - Special Focus on Plant Protection Products" (Focks et al. in press), and guidance on systematic reviews (EFSA 2010). Requirements for this literature review are listed in Table 1 along with specifications on how we addressed them for the current study. A detailed description of the methodology is provided in Singer et al. (2025).

The scientific literature was systematically searched for publications addressing wood mouse biology and population dynamics (see topics in Fig. 1 that abbreviate the search terms shown in Singer et al. 2025). We searched using Google Scholar for predefined keyword combinations that were guided by the characteristics from Pop-GUIDE Phase 2. Pop-GUIDE characteristics capture the topics that are relevant for the mechanistic representation of population dynamics. We logically combined Pop-GUIDE characteristics that represented similar topics and abbreviated the search terms to capture a broad range of word forms (e.g. adjectives, verbs and nouns).

The initial results of the searches were screened for relevance to our review: publications were required to address relevant aspects of wood mouse ecology, present original data from European study sites and include a full description of the methodology (which excluded review articles). Only publications in English were included in the review. Publications identified as not relevant for the review were recorded along with the reason for their ineligibility.

From the eligible publications, we extracted information on the Pop-GUIDE characteristics using a template table. For this purpose, we combined Pop-GUIDE characteristics (e.g. characteristics 'life span' and 'survival rate' were grouped as 'Mortality/Life expectancy') to achieve clearly distinct groups. We additionally introduced the characteristic 'Diet' (Fig. 2). Further, the characteristic 'environmental condition' was recorded as meta-information because it can potentially affect different types of ecological endpoints. Many publications contained information on several characteristics, and each information item was recorded with respect to its characteristics, i.e. multiple entries per publication were included in the table. Therefore, the information items, instead of the publications, became the entities of the literature review. Each information

Table 1. Literature review requirements and how they were addressed.

Requirement	Methodological approach
General review methodology	
Transparency and reproducibility*+	1.) Predefined literature review protocol (Singer et al. 2025)
	2.) Documentation of review steps and outcome
Literature search	
Transparency and reproducibility*+	1.) Publicly accessible search engine
	2.) Predefined search terms
Focused on wood mouse population modelling (relevance)$§	Search terms focused on 1.) wood mouse (*A. sylvaticus*) 2.) population modelling – guided by Pop-GUIDE characteristics
Comprehensiveness§	1.) Separate searches for the different Pop-GUIDE characteristics
	2.) Comparison of search results with references cited in standard literature on wood mouse ecology and modelling (Singer et al. 2025)
Literature screening, literature review and data extraction	
Transparency and reproducibility*$§	1.) Documented, automated and standardised procedures for storing and cleaning the literature database
	2.) Eligibility criteria ensuring reliability and relevance (Singer et al. 2025)
	3.) Predefined templates and procedures for a) Listing ineligible publications b) Extracting information
	4.) Distribution of publications among five reviewers with complementary relevant expertise (Singer et al. 2025)
	5.) Training and cross-evaluation of reviewers
Focus on wood mouse population modelling (relevance)$§+	Information extraction and categorisation according to Pop-GUIDE characteristics. See the characteristics in Fig. 2.
Comprehensiveness§	All the literature identified by the search engine was screened and, if relevant, reviewed for data extraction.
Literature summary	
Transparency and reproducibility*$§+	Extracted information was summarised by one reviewer. The summary was revised by a second independent reviewer.
	The summary is documented as part of the conceptual model (Suppl. material S1).
Focus on wood mouse population modelling (relevance)$+	Extracted information was summarised to inform the decision steps of Pop-GUIDE (Phase 3).
Comprehensiveness§	All extracted information was considered during the summary.

* EFSA (2010); § EFSA Panel on Plant Protection Products and their Residues (PPR) (2014); $ (Goussen et al. in press); + Raimondo et al. (2021).

item was recorded with meta-information on methodology and environmental conditions. The meta-information supported evaluation of data quality as well as comparison of information extracted from different studies.

In Fig. 1, the number of search results per characteristic is shown. In addition, the figure shows the cumulative number of publications retrieved after initial screening and removal of duplicates from multiple searches. In the subsequent screening step based on the full text of the search results, publications were removed according to eligibility criteria, mainly because they did not report original peer-reviewed research or did not focus on the wood mouse. After the screening step, 509 publications remained, and the full texts were reviewed. Another 153 publications were excluded during the review of the full texts according to the eligibility criteria, e.g. because they reported on studies focusing on parasites of wood mice or community studies with minor or unresolved

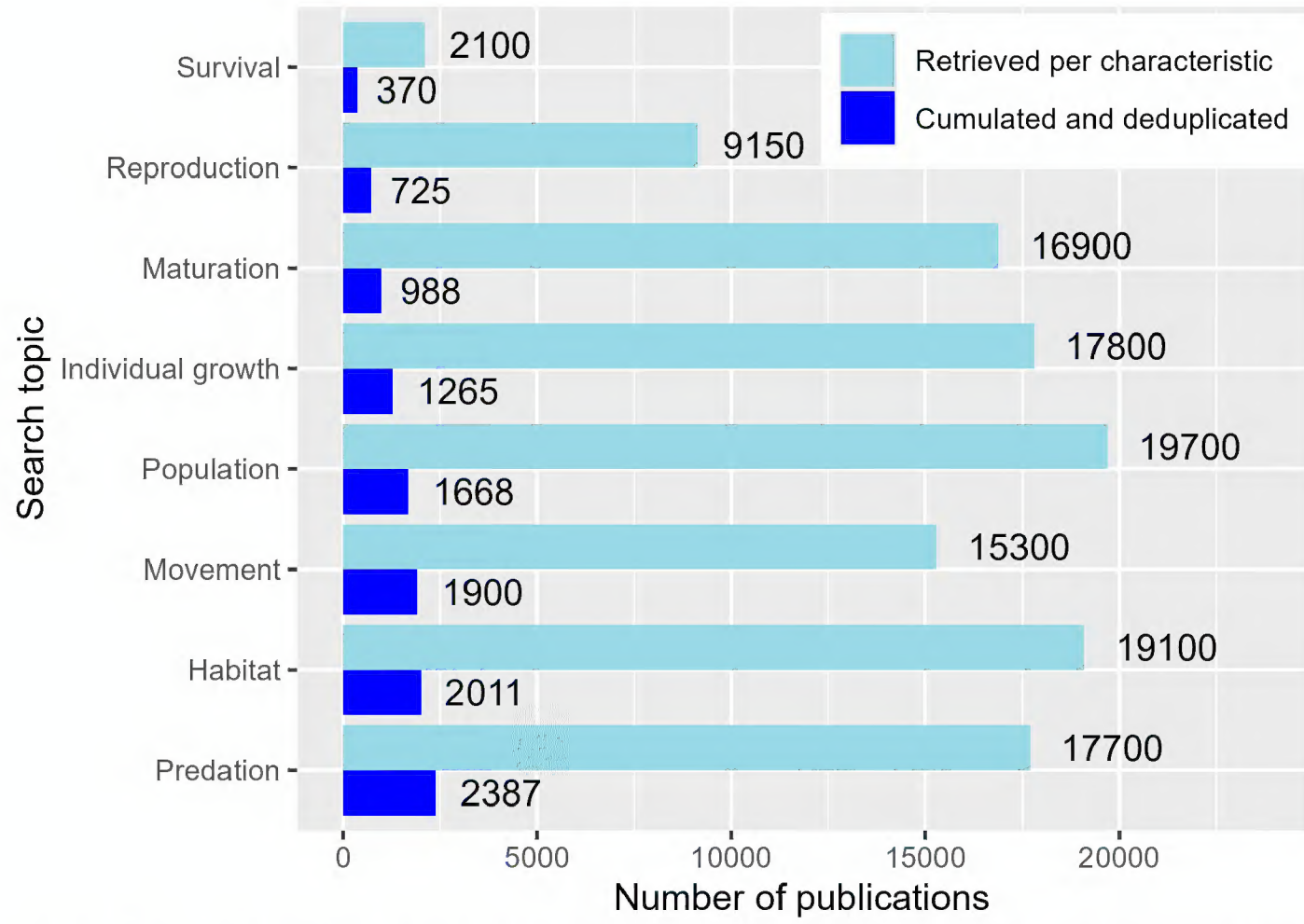

Figure 1. Number of publications returned as results from separate searches specific for each characteristic (light blue bars) and cumulative number of publications retrieved after initial screening (dark blue bars).

contributions of wood mice. In addition, one study, for which the full text could not be retrieved, and 15 publications written in a language other than English were excluded from the review. All publications that were deemed ineligible were recorded together with the ineligibility reason. A total of 341 publications were reviewed in detail. In Singer et al. (2025), details of the literature search, including the eligibility criteria, are documented.

From the 341 publications reviewed, 1295 data items were extracted (Fig. 2) and recorded (Singer et al. 2025). For most characteristics, information from at least 30 publications was identified (Fig. 2), suggesting sufficient data to inform the model. Notably, these publications might have reported different relations or parameters that jointly contributed to the understanding of the characteristics. In contrast, information on wood mouse physiology, particularly ontogenesis and maturation, was scarce (Fig. 2). However, such data were important to inform the construction of the dynamic energy budget sub-model (DEB; see “Phase 3 and Phase 4: Conceptual model for wood mouse populations (APODEMUS)”). In a search dedicated to identifying publications relevant to ontogenesis, additional studies were identified and used, whereby data from related species were also considered.

Phase 3 and Phase 4: conceptual model for wood mouse populations (APODEMUS)

In this section, we present the conceptual model for APODEMUS as derived according to the previously described steps. We describe which modelling decisions were taken following Pop-GUIDE and on which evidence base. Fig. 3 provides an overview of the conceptual model. The full conceptual model description is provided in Suppl. material 1, including the dichotomous decisions taken according to Pop-GUIDE Phase 3.

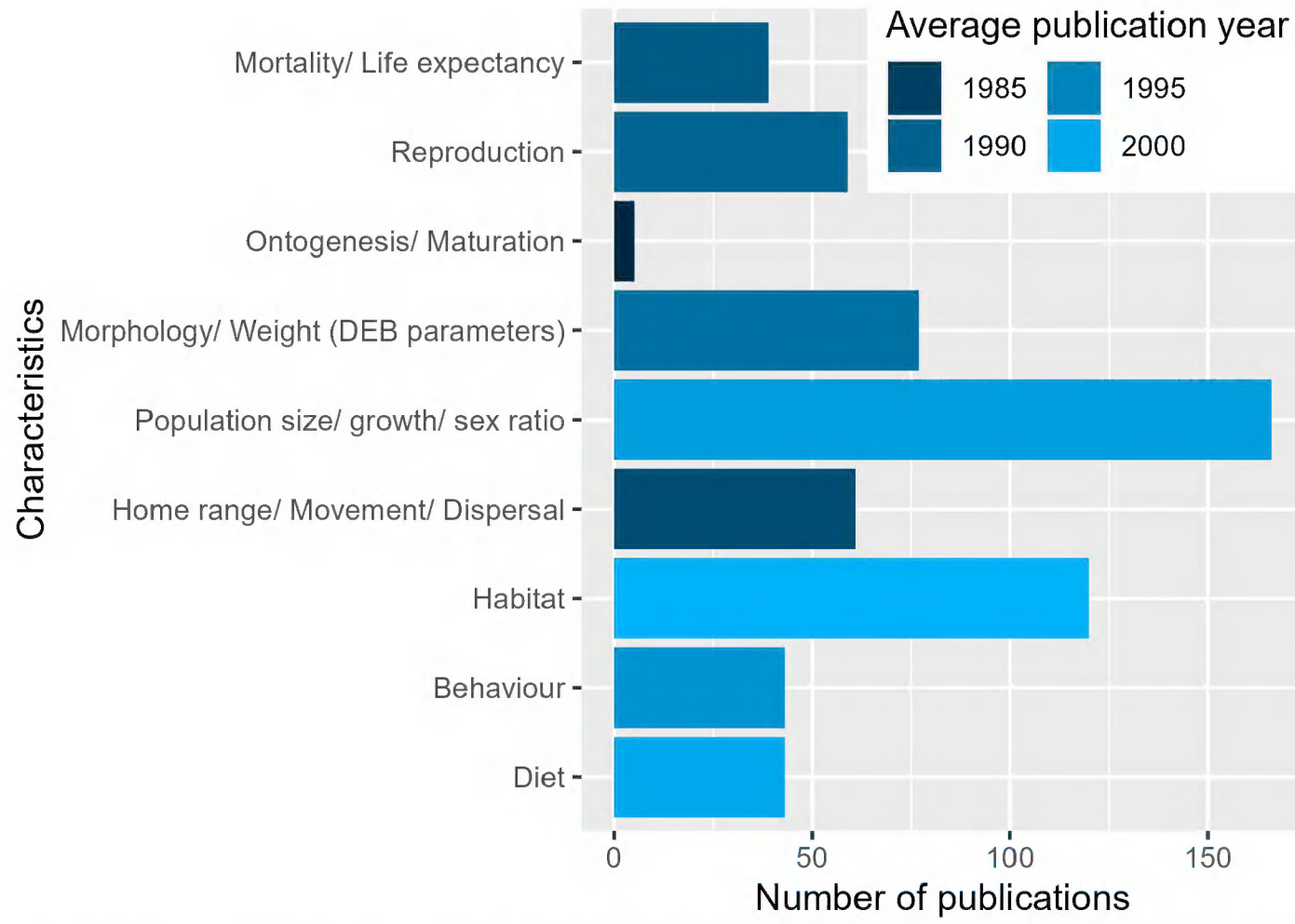

Figure 2. Number of publications providing at least one data item to inform a population model characteristic for the wood mouse.

Life history and organism-level processes

The life cycle of the wood mouse is represented in detail in APODEMUS, including foetus, newborn, juvenile and adult life stages, via the dynamic energy budget (DEB) model. Growth, maturation and reproduction are captured explicitly in the model, making DEB a strong basis for the simulations of toxic effects since body weight across life stages as well as reproductive output has been reported from standard laboratory toxicity studies with surrogate species (EFSA PPR et al. 2018). The DEB model combines these physiological processes in a single mechanistic model based on general bioenergetic concepts (Kooijman 2009). DEB describes the uptake of energy from food (see “Diet”) and the allocation of that energy to maintenance, growth, maturation or reproduction, according to the organism’s needs over time.

Many aspects of DEB models are universal across all organisms, but the general framework is divided into variants for different life histories. The ‘stx’ variant (Marques et al. 2018; Kooijman et al. 2020) is the relevant model for placental mammals, which includes a dependent foetus and neonate (suckling) phase for offspring development. Data gathered for the wood mouse included laboratory growth curves of males and females at different feeding levels, field growth curves, laboratory reproduction data, as well as general life history descriptors from literature sources (Asdell 1946, 1993; Flowerdew 1972; Jones 1982; Grzimek 1990; Corbet and Harris 1991; Gerlach and Bartmann 2002; Balčiauskienė et al. 2004; Monarca et al. 2020). These data allowed the fitting of model parameters for male and female animals, the parameterisation of a mammalian reproduction model previously developed for the Wistar rat (a laboratory strain of the Norway rat), and the option to model the response to restricted feeding.

The wood mouse gestation period is around 23 days (Asdell 1946; Grzimek 1990; Corbet and Harris 1991), followed by around 21 days of lactation

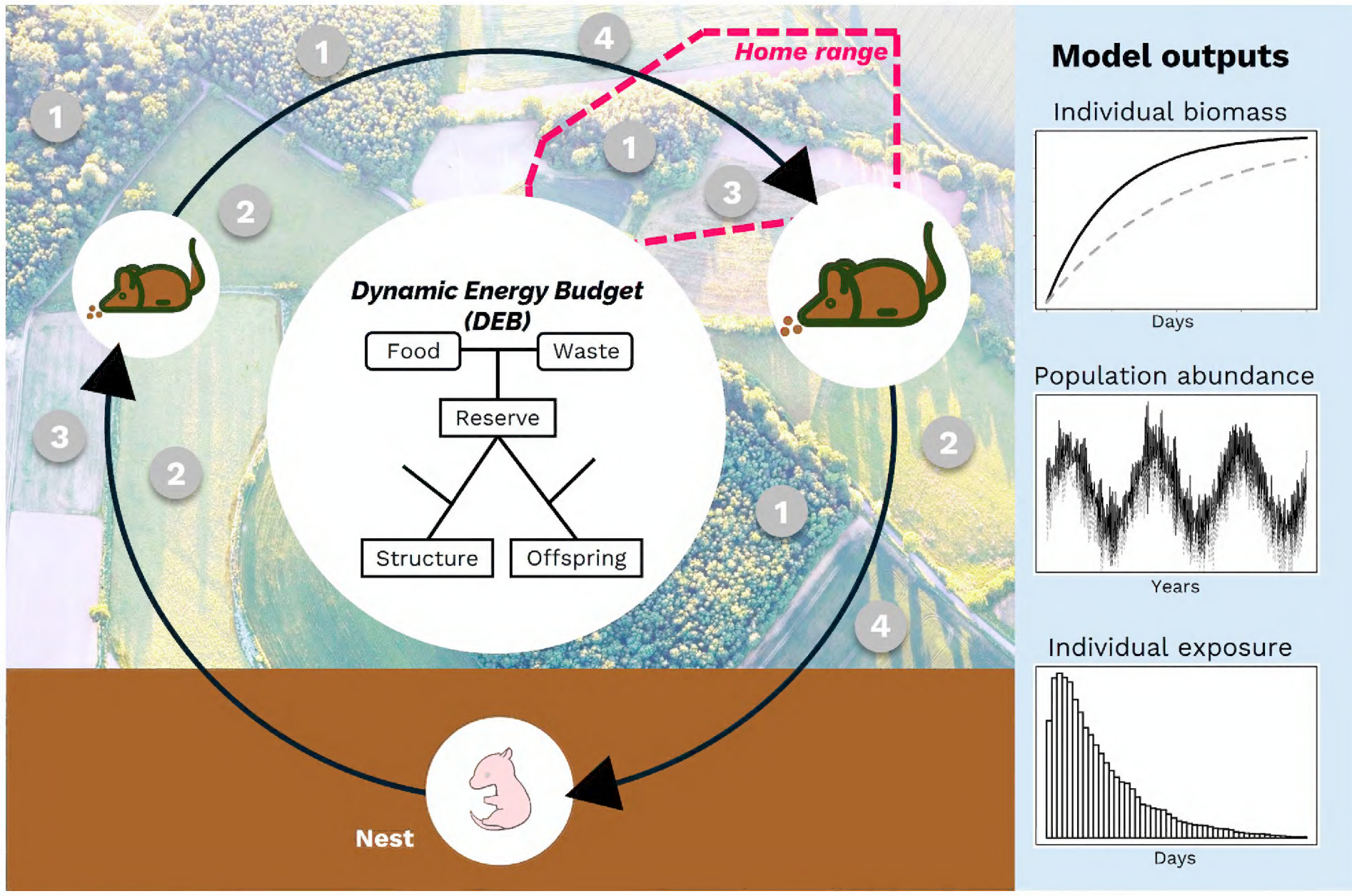

Figure 3. Overview diagram of the conceptual population model for APODEMUS. The model simulates the wood mouse life cycle, growth and reproduction. Landscape composition is captured by habitat types (numbers) and influences the space use of the simulated wood mice. Exposures can be linked to the use of defined habitat patches and types.

(Grzimek 1990; Corbet and Harris 1991; Monarca et al. 2020). Male wood mice reach sexual maturity at around seven weeks of age in the laboratory (Corbet and Harris 1991), while females are mature after eight weeks (Gerlach and Bartmann 2002). Laboratory data show that dominant or solitary females produce, on average, 3–4 litters of 5.6 young over 120 days, with an average interbirth interval of 26.5 days (Gerlach and Bartmann 2002). This suggests that mating occurs shortly after birth and females become pregnant during lactation. During the dependent foetus and neonate life stages, offspring have their energy needs supplied by the mother, which upregulates feeding (Makarova et al. 2017; Rakel et al. 2022).

In the DEB model, we assumed that all simulated mice can fulfil their energy needs at all times, i.e. we did not consider food limitation as an initial simplifying assumption. Energy limitation linked to food availability in the landscape may be considered in extensions of the model. The DEB model simulates the individual growth and maturation of wood mice. Instead of growth, mature wood mice use their energy intake for maintenance and reproduction. In mature females, feeding is upregulated, and the additional energy enters a storage compartment, the ‘reproduction buffer’, which goes towards the growth and maturation of the dependent offspring (during pregnancy and lactation). Thereby, two concurrent litters (one suckling and one in the womb) can be simulated by partitioning the reproduction buffer.

Population and spatial factors

Habitat use

A defined objective of higher-tier risk assessment of small mammals, and thus of APODEMUS, is the estimation of exposures to pesticides and their potential effects on individuals and populations in realistic landscape settings. Pesticide applications result in variable exposures over time and across habitats. Wood mice have been reported to use several habitats, whereby usage depends on habitat type (Zhang and Usher 1991; Tattersall et al. 1999; Moore et al. 2003; Carvalho and Gomes 2004; Klaa et al. 2005; Alain et al. 2006; Heroldová et al. 2007; Loman 2007; Panzacchi et al. 2010; Noguerales et al. 2015; Janova and Heroldová 2016; Balestrieri et al. 2017; Occhiuto et al. 2021), season (Hansson 1968; Green 1979; Fitzgibbon 1997; Kotzageorgis and Mason 1997; Todd et al. 2000; Butet et al. 2006; Janova and Heroldová 2016; Occhiuto et al. 2021; Savazza et al. 2023), and management (Tattersall et al. 2001; Fischer and Schröder 2014; Bryja et al. 2000; Bergstedt 1966; Fitzgibbon 1997, but see Loman 1991a).

An agricultural landscape comprises different types of habitats, including, but not limited to, arable fields (pesticide-treated and untreated), pastures, woods, shrublands or hedgerows. With male home range areas reaching up to 2 ha in agricultural landscapes during the breeding season, and female home ranges up to 0.5 ha (Table 2), a single wood mouse can use several habitats of differing types on a regular (daily) basis (Kikkawa 1964; Watts 1970; Fitzgibbon 1997; Panzacchi et al. 2010). As a generalist species, wood mice are assumed to feed on various diet items present in each habitat type they visit. Accordingly, a mouse can be exposed to a pesticide through its diet if it uses a pesticide-treated field for foraging or adjacent habitats potentially exposed to spray drift, dependent on the pesticide application type. Thus, the model requires an explicit representation of the landscape composition and its use by wood mice, as recommended in the higher tiers of bird and mammal ERA (European Food Safety Authority 2023).

Table 2. Home range sizes of male and female wood mice in agricultural landscapes. Mean ranges and sample size (brackets) are listed unless otherwise specified. Home ranges were measured by radio-tracking and calculated with a restricted polygon or kernel method. All studies were conducted in the UK; sd – standard deviation of the mean; se – standard error of the mean.

Season	Life stage	Home range (m^2)		Citation
		Male	Female	
Breeding season	Adult, > 20 g	Home range per individual: 18125; 23300 (n = 2)	Home range per individual: 1338 (n = 1)	Tew et al. (1992)
Breeding season (May–Aug.)	Adult, > 23 g	Nightly range (min convex polygon): ca. 12500 (n = 7)		Dell'Omo and Shore (1996)
Before harvest (winter cereals) (Aug.)	Adult	7600; sd = 8900 (n = 6)		Tew and Macdonald (1993)
After harvest (winter cereals) (Sep.)	Adult	4900; sd = 5200 (n = 6)		Tew and Macdonald (1993)
Before harvest (winter cereals, winter beans, set-aside) (Jun.–Jul.)	Adult	18700; se = 3800 (n = 9)	5500; se = 2800 (n = 7)	Tattersall et al. (2001)
After harvest (winter cereals, winter beans, set-aside) (Sep.–Nov.)	Adult	1900; se = 500 (n = 9)	1400; se = 700 (n = 9)	Tattersall et al. (2001)

The heterogeneous landscape is represented in the model as a grid whereby each grid cell is assigned to a habitat type. The resolution of the grid can be adapted, e.g. according to the resolution of the available landscape data. It is assumed that each habitat type is homogeneously attractive because limited information is available about heterogeneity within habitat types and the use of micro-habitat structures by wood mice, particularly for open habitats (but see Tew et al. 2000). The spatial representation makes it possible to capture exposure heterogeneity within a treated field (or other exposed habitat) which could occur, e.g. due to precision farming applications.

In the model, use of habitats within the home range of a wood mouse depends on the attractiveness of these habitats. We assumed that habitats of similar types are similarly attractive to the mice. Habitat attractiveness is described by a one-dimensional index which is an input to the model. In the model, the habitat index drives the location and extent of wood mouse home ranges (see Movement). The index subsumes known or estimated abiotic and biotic habitat features that are relevant for wood mice, for instance, vegetation structure or litter (Tew et al. 2000; Boyard et al. 2008; Dorigo et al. 2021), food availability (e.g. seeds, other plant matter or arthropods; Sozio and Mortelliti 2016), or species interactions (e.g. competition or predation, see "External factors"). Further, the index can vary over time, reflecting seasonal changes in the attractiveness of habitats. The attractiveness of a habitat might vary due to changes in habitat features as well as changes in the needs of the wood mouse. Finally, habitat use by wood mice is context-dependent because their wide spatial-ranging behaviour allows them to flexibly choose among alternative habitat types in a landscape. Therefore, the preference for a habitat type varies with the availability of alternatives. In the model, use of certain habitat types depends on their attractiveness relative to each other. Woody habitat is considered a standard for the habitat index because this habitat type is constantly used throughout the year (e.g. Kikkawa 1964; Zhang and Usher 1991), and woody structures improve the suitability of off-crop habitat for wood mice (Tattersall et al. 2001; Alain et al. 2006; Butet et al. 2006; Boyard et al. 2008; Ruiz-Capillas et al. 2013; Noguerales et al. 2015). In the model, temporally changing habitat attractiveness of other habitat types can be gauged relative to the attractiveness of the baseline woody habitat.

We assumed that modifications of habitats by wood mice are negligible because they are not known to engineer or critically overuse their habitat. Accordingly, the habitat index is not changed by the simulated wood mice, and the wood mouse population dynamics depend on the available habitat, but feedback (as discussed in Linder et al. 2012) of wood mice on their environment can be ignored.

The habitat index can be parameterised from available data. Specifically, extensive capture–mark–recapture studies (e.g. Janova and Heroldová 2016) provide information on wood mouse densities across habitat types in agricultural landscapes. Even though none of the reviewed studies sampled wood mice in all available habitat types, combining study results provides a solid picture of seasonal relative habitat attractiveness. Further, improved mechanistic models on the use of habitat features by wood mice can be implemented as a sub-model to the index layer if respective information becomes available in the future. Finally, construction of ERA model application scenarios can involve manipulating habitat indices to test the sensitivity of model outputs, including toxicant impacts, to landscape configurations.

Movement

Wood mouse spatial behaviour has extensively been studied in large-scale and long-term ecological field studies. But detailed information on movement behaviour and patterns was available only for a few habitat types. Generally, the movement of female mice was described by a correlated random walk (Jamon 1994) with deviations from this pattern (Benhamou 1990) in response to distant landmarks as movement targets (Sozio et al. 2013), linear structures (Zhang and Usher 1991; Galantinho et al. 2020) and guiding paths (Benhamou 1990; Jamon 1994). In addition, wood mice were reported to use burrows (Jennings 1975; Pelz 1979) to which they return after and often multiple times during (mostly nocturnal) activity periods (Wolton 1983, 1985). Motivations for movement decisions such as stops or returning to the burrow were not described, which adds uncertainty to movement predictions.

In contrast to detailed movement patterns, more information was available about wood mouse home ranges, i.e. space use at a higher, aggregated level. Information on the size and shape of home ranges was available for several landscape types, including agricultural landscapes (Table 2). Home ranges reflect the spatial extent of regular movements over multiple days or weeks (Wolton 1985). Depending on the definition and measurement methodology, home range information might even comprise infrequent excursions (i.e. movements over larger than average distances; see Crawley 1969 for a categorisation of wood mouse movement types). As methodology and result interpretation differed among studies, the distinction between regular and excursion movements appeared subjective.

To a lesser extent, temporal information on home range stability and change was found in the literature. Even though home ranges seemed usually to be stable (e.g. Wolton 1985; Attuquayefio et al. 1986; Korn 1986; Canova et al. 1994; Fernandez et al. 1996; Godsall et al. 2014), home range or nest site shifts occurred mainly during the breeding season (Randolph 1977; Green 1979; Wolton 1985; Halle 1993) or were triggered by disturbance (particularly harvest and ploughing in arable fields; e.g. Green 1979; Pelz 1979; Loman 1991a; Tew and Macdonald 1993; Tattersall et al. 2001). Further, sex influenced home range behaviour. The larger home ranges of males during the breeding season (Table 2) were associated with access to potential mating partners. Thereby, male home ranges showed considerable overlap and also overlap with female home ranges (Montgomery 1979; Wolton 1985). In contrast, during the breeding season, females were reported to exclude conspecific females from their home ranges (Montgomery 1980; Wolton 1985; Halle 1993; Sunyer et al. 2016).

In APODEMUS, wood mouse movement is aggregated into the representation of home range dynamics due to the more abundant and reliable information on home ranges. Each mouse can establish a home range and adjust it in size and shape to fulfil its needs. Thereby, the habitat parts are included within a home range provision to these needs, depending on their momentary attractiveness (habitat indices are provided as inputs to the model; see Habitat use). Home ranges comprised of highly attractive habitat (with abundant resources and cover reflected by high habitat indices) can be smaller than home ranges comprised of inferior habitat. Further, during the breeding season, wood mice in the model respond to the presence of females in the vicinity. Males aim at

including these females in their home range, while females aim at excluding them. If the available space and environmental conditions are insufficient to establish a home range (particularly females) at a specific location, wood mice move within the modelled landscape in search of a suitable spot at the cost of losing dependent offspring (females), suppressed breeding and increased mortality. For details, see Suppl. material 1.

Diet

Consideration of the diet of wood mice was important for the model because diet represents the route of pesticide exposure addressed by the model (see "Exposure and effects characteristics"). Wood mice were reported to consume a broad diet, including seeds, fruit, leaves and other green plant material, roots, acorns, chestnuts and other tree seeds, arthropods, earthworms and fungi (e.g. Hansson 1971; Flowerdew and Gardner 1978; Green 1979; Montgomery and Montgomery 1990; Canova 1993; Rogers and Gorman 1995; Abt and Bock 1998). Thereby, the consumption appeared to be mainly driven by food availability rather than preferences for specific food types. Mice consumed most food items presented in an experimental setting ('cafeteria experiment'; Gasperini et al. 2018), and stomach content studies indicated seasonal diet compositions corresponding to the availability of food items at the study location and season (Hansson 1971; Green 1979; Montgomery and Montgomery 1990; Rogers and Gorman 1995; Abt and Bock 1998).

In the current concept for APODEMUS, we assumed that wood mice can always fulfil their daily energy needs from the food available in the landscape. The assumption was supported by the broad diet of wood mice and their mobility, which indicated a high flexibility to find food in a landscape across seasons. This simplifying assumption means that simulated wood mice cannot starve. Rather, they shift their home ranges to cover seasonally productive habitats. Consequently, habitat use is indicative of the consumed diet: the time spent during the daily activity period of a mouse in each habitat type corresponds to the diet intake from that habitat. Accordingly, pesticide exposure is driven by an individual's temporal pattern of habitat use (see "Exposure and effects characteristics").

The model could be extended in the future to explicitly consider seasonal food availability in habitat types. Food availability would affect the energy consumption of individual wood mice in the model and, consequently, their development and reproduction. Such further development of the model would make it possible to assess potential interactions between food limitation and pesticide effects as well as potential indirect effects of pesticides causing reduced food availability. However, information or estimates of food availability by habitat type and season would be required along with the energy content of various food items and their accessibility as well as the assimilation efficiency by the wood mouse.

Density dependence

In the wood mouse, negative density-dependent regulation of populations was described whereby higher densities appeared to impact subsequent population growth rates (Bengtson et al. 1989a; Díaz et al. 2010; Flowerdew et al. 2017).

Processes driving density dependence in the species were less clear from the literature, with food limitation, limited movement ranges, suppression in reproduction, increased pathogen and parasite load and predation suggested as possible mechanisms. However, correlations of these factors with population densities were not observed consistently across studies (Erlinge et al. 1983; Bengtson et al. 1989b; Montgomery et al. 1991; Díaz et al. 2010; Sozio and Mortelliti 2016; Flowerdew et al. 2017). Female home ranges were reported to be non-overlapping (see "Population and spatial factors – Movement"), resulting in space as a limiting factor for population density (Montgomery 1979; Wolton 1985; Cassaing et al. 2013). Exclusive home ranges of females were included in APODEMUS, and thus density dependence can emerge in the model.

Behaviour

Beyond the explicit use of the landscape by individuals, no wood mouse behaviours are represented in APODEMUS. During the model development, behaviours were considered that could potentially interact with individual-level exposure or population dynamics in the model, including social (e.g. aggressive) interactions, infanticide, food caching (or hoarding) and dehusking (Lambin 1988; Loman 1991b; Wilson et al. 1993; Polechová and Stopka 2002; Brühl et al. 2011). The importance or frequency of these behaviours across wood mouse populations could not be derived from the identified literature. Social and aggressive interactions as well as infanticide are implicitly included in the model through the representation of exclusive female home ranges and the suppression of reproduction in females without established home ranges (see "Population and spatial factors – Movement"). Although not included in the conceptual model, food caching and dehusking could potentially interact with individual-level exposure in specific cases. Such cases could be considered by developing relevant simulation scenarios rather than inclusion as explicit processes in the model.

External factors

External factors affecting populations (other than the chemical stressor of interest) can include interactions with other species and with the abiotic environment. From the literature, no specialised interaction with other species was reported, i.e. the wood mouse was assumed to have no obligatory relationships or predators specialised on it as prey. While predation is an important factor in wood mouse survival, no quantitative link could be established for occurrences. In addition, weather could directly influence wood mice, but a quantitative link could not be established from the literature (see "Life history and organism-level processes").

Thus, the model implicitly includes predation in the background mortality. Variability in external factors is also implicitly accounted for in the assignment of seasonally variable habitat indices (see "Population and spatial factors - Habitat use"). With the landscape input, variability in habitat suitability within and across years can be represented. Accordingly, indirect effects of weather and agricultural management on habitat suitability (including food availability) can be captured by the model.

Breeding seasons of the wood mouse were reported to vary across European regions, with mice usually not reproducing in the winter in central Europe (Flowerdew 1972; Green 1979; Jamon 1986; Halle 1993, but see Smyth 1966; Montgomery et al. 1991 for records of occasional winter breeding) and northern Europe (Bergstedt 1965). In southern Europe, reproduction was reported to continue through the winter months (Moreno and Kufner 1988; Díaz and Alonso 2003; Rosário and Mathias 2004), but breeding was interrupted in summer (Moreno and Kufner 1988; Rosário and Mathias 2004), even though activity in mountainous areas was high in June and July (Jaime-González et al. 2017). Although this indicated that the breeding season in wood mouse populations may be temperature-dependent, quantitative triggers for the initiation or cessation of breeding were not identified. Thus, the breeding season is defined by model parameters rather than environmental forcings. Different breeding season timings and durations will be investigated by scenarios in which these parameters are varied.

Exposure and effects characteristics

The conceptual model development presented in the current paper focuses only on the representation of wood mouse ecology in APODEMUS. However, exposures and effects must be considered during model development to assure that the model will be ultimately fit for purpose, i.e. for use as a tool in higher-tier risk assessments. Here, we provide generic considerations with respect to exposure and effects of a pesticide, not addressing a specific compound or application type. In the model, exposure of individual mice is addressed through their diet (see “Diet”). The proportion of time spent during the daily activity period of a mouse in a habitat type with exposed food corresponds to the intake of exposed food during that day. Thus, the effective exposure of an individual is determined by the total daily food consumption rate of a wood mouse, the proportion of time spent in habitats with exposed food, and the exposure concentration in the food. Thereby, the exposure levels can vary temporally and spatially across the landscape. The environmental presence of pesticides varies with their physicochemical characteristics and fate in various media, application type, agricultural practice, habitat type (or crop), environmental conditions and date. Data on environmental exposure can be specified as input to the model in the form of time series for each habitat. This approach provides flexibility to analyse different ERA scenarios.

Organism-level effects from dietary exposure to pesticides are assessed in toxicity studies with surrogate species, most commonly the Norway rat (OECD 2001, 2018a, 2018b). In standard toxicity studies, lethal and sublethal effects are quantified. Sublethal endpoints measured include, for instance, body weight over time, pregnancy rate, litter size and pup weight. Additional endpoints measured in toxicity studies may depend on the tested compound and study type. Their relevance for the population model will need to be reviewed. For instance, hormone levels may be correlated with other sublethal measurements and cannot be represented explicitly in the model because physiological processes are currently not considered in such detail.

While exposures are kept constant in laboratory toxicity studies, exposure levels of individual wood mice in an agricultural landscape are expected to vary between individuals and over time. For example, exposure to treated seeds

may only occur for a limited number of days after sowing. To capture individual-level effects of time-variable exposures, individuals are equipped with a toxicokinetic–toxicodynamic (TKTD) sub-model linked to the DEB model used to represent individual-level physiological processes (see "Life history and organism-level processes"). Thereby, the toxicokinetics (TK) could be represented using a more detailed approach, a physiologically based kinetic (PBK) module, which mechanistically captures physiological and biochemical processes in an organism and simulates the movement of substances through multiple compartments corresponding to organs and tissues. TKTD models are specific to a compound, and thus, this effect sub-model requires calibration and testing for each compound addressed.

Specifics of the concept for the implementation of pesticide exposures and their effects require detailed review of compound-specific information, such as pesticide application types, modes of action and fate in the environment, as well as endpoints measured in laboratory toxicity studies. These need to be carefully considered in every application of the model to a new compound.

Phase 5: Model implementation and evaluation

The conceptual model provides a schematic for model implementation, detailing the processes included in APODEMUS. For the implementation of the model, the conceptual model has to be formalised for direct translation into computer code (EFSA Panel on Plant Protection Products and their Residues (PPR) 2014). For the documentation of the implementation of the individual-based model, we will follow the ODD protocol (Grimm et al. 2006, 2020). Parameter values and their ranges must be determined from literature sources. For this purpose, we will rely on the literature compilation (see "Phase 2"). Some parameters may not be directly reported in the literature but may need to be derived, e.g. by estimating averages and ranges from multiple published studies or converting from reported temporal or spatial scales to relevant scales for the model. The detailed description of the model implementation as well as the parameterisation will be incorporated in TRACE documentation (Schmolke et al. 2010; Grimm et al. 2014). The TRACE documentation will also include the description of model evaluation. These standards for model documentation are recommended by the EFSA Panel on Plant Protection Products and their Residues (PPR) (EFSA PPR 2014) and Becker et al. (2024). The model code will be commented on systematically and comprehensively (Becker et al. 2024), and documentation will be made publicly available.

During model development, it is crucial to consider how the implemented model can be evaluated with respect to its usefulness for the intended purpose and domain of applicability. Patterns of wood mouse populations reported in the literature, e.g. seasonal population sizes and structures, can be compared to model outputs using, for example, pattern-oriented modelling (POM; Wiegand et al. 2003; Grimm and Railsback 2012) or other quantitative methods. Variability in populations will be partially captured by model stochasticity, which reflects reported variability in processes explicitly represented in the model. For instance, reported ranges of litter sizes will be included by assigning a litter size to each simulated female, which is drawn from a literature-informed distribution. In addition, the influence of parameter values on model outputs can

be addressed in a sensitivity analysis, considering the value ranges determined from the literature. That way, it can be determined how parameter uncertainty translates into model output uncertainty, and parameters can be identified which are most impactful to model outcomes.

The wood mouse population model is intended for application in higher-tier risk assessments of pesticides. Potential exposures via residues in food and their acute and long-term effects should be simulated in agricultural landscapes. Accordingly, the implemented model should be evaluated with data from studies of wood mice in such landscapes. Study data that could be used for model evaluation are assumed to be limited in temporal and spatial extent, and observations may be specific to study design, location or region, and season. Field studies conducted for pesticide risk assessments use different standardised study designs which require rigorous selection of study sites with multiple locations acting as replicates. However, the studies are often specific to a crop of interest and limited to individual fields and their immediate vicinity. One study type used in the context of higher-tier pesticide risk assessments addresses the daily proportion of time spent in a crop of interest by an animal (PT study), used as a proxy for the daily diet obtained from the crop fields. In such studies, small mammals, including wood mice, trapped initially in the field or along its edge are fitted with a radio transmitter. Individuals are then tracked for an entire nocturnal activity period to obtain data on their use of the crop fields and adjacent areas. Studies are generally conducted within a short period, which corresponds to the pesticide application timing. Similarly, in acute field effect studies, individuals of small mammals trapped in or along the edge of crop fields are equipped with radio transmitters shortly before the application or drilling of treated seeds and repeatedly checked for 7–10 days after the application or drilling. The focus of these studies is proof of exposure in treated fields and determination of the individual fate, i.e. survival, after exposure. Usually, data from untreated control fields and treated fields are compared to take natural mortality and emigration from fields into consideration. In long-term field effect studies, populations are observed over longer periods, and these studies follow a capture–mark–recapture design. Traps are set up in defined locations within treated fields, untreated control fields and adjacent non-crop habitats. Multiple trapping sessions are conducted over an entire season. Animals are individually marked for recognition when they are first caught or identified in subsequent trapping sessions. In addition, their weight, sex and reproductive status are recorded. Here, potential long-term and reproductive effects of exposure in the treated fields can be assessed through abundance measures and population parameters.

Data from all three study types can be used for model evaluation. Daily time spent in focal fields by individual simulated mice can be an output of the model, and spatial patterns can be compared to PT studies. Thereby, simulations can use the landscape composition of a study. Data from simulated individuals can be retrieved, focusing on mice with home ranges overlapping with the field and their use of the field during the date range corresponding to the study. Similarly, these data can be used for comparisons with acute-effect studies and the reported exposure. In addition, survival of single individuals after exposure in treated fields and from control fields can be compared to field data. For the simulation of long-term field effect studies, virtual trapping can be introduced in the model. Traps in locations corresponding to those in a study can

be simulated, and mice are “caught” with a certain probability if they spend time in the corresponding habitat patch. Mouse capture numbers per trapping date can be compared to study data as well as the recapture rate. In addition, relative changes in population sizes can be compared between populations around treated and control fields as well as population dynamics over time.

Stakeholder involvement: expert group and workshop

The involvement of stakeholders in the modelling cycle has long been recognised as important for model relevance and acceptance for regulatory and management purposes (e.g. Jakeman et al. 2006; Schmolke et al. 2010; Singer et al. 2011) and is also recommended in Pop-GUIDE (Raimondo et al. 2021). However, stakeholder involvement can be difficult to achieve in practice. Involvement of stakeholders requires substantial time investment on their part. In addition, for model development in regulatory environmental risk assessments, obstacles can be the diversity of interests, expertise and jargon among various stakeholders from different sectors (e.g. regulatory agencies, academia or industry) or with different backgrounds (e.g. ecological sciences, statistical and computer modelling or environmental risk assessment). Considerations of impartiality can also limit the involvement of stakeholders, particularly regulators.

Despite these challenges, we had the unique opportunity to garner interest from multiple regulators, small mammal experts and ecological modellers who committed to taking part in the modelling cycle and participating in a workshop dedicated to the conceptual model of APODEMUS. The workshop with the expert group was hosted by RIFCON GmbH (Hirschberg, Germany) from 28–29 February 2024. The aim of the workshop was to ensure a relevant representation of wood mouse ecology by the model in the context of higher-tier risk assessment. Specific pesticide exposures and effects were not discussed during the workshop.

The workshop focused mainly on decisions in the conceptual model for which information from the literature was lacking or ambiguous but important in the context of the model objectives. The discussions during the workshop helped refine the representation of processes and identify remaining uncertainties. The summary of the workshop is provided in Suppl. material 2. In addition to the considerable refinement of the conceptual model, the stakeholder workshop improved the communication and transfer of expertise between different stakeholder groups. Thus, the stakeholder workshop imparted learnings about species ecology, mechanistic modelling and regulatory needs to all participants and benefited the process of model development, evaluation and application.

The expert group will be further consulted in Phase 5 of the model development, providing input and feedback on technical, ecotoxicological or regulatory issues that might arise in the context of model implementation, parameterisation, testing and scenario development.

Suggestions for Pop-GUIDE improvement

Pop-GUIDE defines a procedure that applies to the development of population models irrespective of organism, geographic region or risk assessment objective addressed. However, risk assessments of species listed as threatened or endangered in the US statute were used as an example (Raimondo et al. 2021).

During the development of the conceptual model of APODEMUS for the European risk assessment, we identified limitations of Pop-GUIDE. In the following discussion of the phases of Pop-GUIDE for APODEMUS, we describe our experiences and suggest refinements of Pop-GUIDE.

Generally, we think it would be beneficial to consider existing models explicitly in the early stages of model development. In many cases, population models are not developed without precedents, i.e. published models are often available for the species, species with similar ecologies or similar domains of applicability. Review of existing models can support model development in several of the Pop-GUIDE phases. Understanding and applying existing models to pending ERA questions can reveal the knowledge base and help target future model objectives to the relevant unknowns. Similarly, the literature search can be focused on knowledge gaps, while an update to recent scientific developments is sufficient for previously well-informed parts of the model. Further, existing models can support the development of the conceptual model by providing options for process formulations. Existing model implementations even allow testing process formulations and evaluating their consequences at an early stage of model development. These advantages of existing models play out particularly well if they have been designed following Pop-GUIDE or other structured modelling frameworks. The standardised frameworks ensure that the models' domains of applicability are well documented, and therefore it can be easily assessed whether these models are suitable for a given risk assessment or other applications. Last but not least, this procedure helps to identify data gaps that should be filled by future fieldwork with the target species.

ERA objectives (Phase 1)

Phase 1 of Pop-GUIDE requires the formulation of objectives for the model in ERA. The importance of defining questions and purposes of models has been identified previously as well (e.g. Railsback and Grimm 2019). The clear definition of the objectives facilitated focusing on the domain of applicability of APODEMUS to guide decisions about inclusion and detail of processes.

However, the decision tree provided by Pop-GUIDE to identify the trade-offs among generality, realism and precision of an ERA as part of the definition of objectives (see fig. 1 in Raimondo et al. 2021) is strongly geared toward risk assessments of threatened and endangered species. This decision tree is not straightforward to use for models developed in the context of ERAs in the European Union where threatened and endangered species are currently not considered explicitly in pesticide risk assessments. We suggest including risk assessments according to European Union guidelines as well as other regulations in the Pop-GUIDE decision tree. For the higher-tier risk assessment for birds and mammals (European Food Safety Authority 2023), species common in agricultural landscapes are considered. Abundant data on general ecology may be available for a given focal species used in these risk assessments, which can inform the development of a realistic model applicable across different European regions. However, the risk assessment question needs to be answered for specific pesticide application use cases. These can be summarised in ERA scenarios (EFSA Panel on Plant Protection Products and their Residues (PPR) 2014; European Food Safety Authority 2023; Focks et al. in press). The ERA

scenarios describe pesticide application at the smaller scale of agricultural landscapes and consider local characteristics such as climatic conditions, habitat composition or agricultural practice. Modelling the focal species within ERA scenarios requires precise information on the interaction of the species with the scenarios' characteristics. Thus, realistic–precise models may be indicated at least for some focal species to fulfil ERA requirements, combining the necessity of their domain of model applicability across Europe and the precise representation of ERA scenarios specific to a location or crop.

Literature review (Phase 2)

Pop-GUIDE was used as guidance to conduct the wood mouse literature research. Particularly, the species' characteristics important for population models (Pop-GUIDE Phase 2) ensured the comprehensiveness of the literature search. In the context of small mammals and other terrestrial animals, the characteristic 'diet' is important but lacking in Pop-GUIDE. We included this characteristic in our literature review and suggest adding it as a standard Pop-GUIDE characteristic. Further, we suggest aggregating some of the characteristics which, in the context of the wood mouse, provided redundant information.

Pop-GUIDE suggests a table format for the collection of literature information, along with the indication of the level of realism and precision of the data. In the context of risk assessments of common species, for which data are often available from multiple sources, we suggest expanding this table. To aggregate and compare information from an extensive body of ecological literature, it is important to record the context of each study in detail, as well as the studied entities and methodology (EFSA Panel on Plant Protection Products and their Residues (PPR) 2014; Focks et al. in press, Chapter 4). We used an interactively searchable table format (Singer et al. 2025) to cope with the complex information.

We conducted a comprehensive review of the available ecological literature on the wood mouse, which is a requirement according to the scientific opinion on good modelling practice (EFSA Panel on Plant Protection Products and their Residues (PPR) 2014). We found that the available ecological data are heterogeneous, informing some characteristics and parameters more thoroughly than others. For well-informed characteristics, several studies provided similar information. This redundancy fosters trust in model parameter values but does not contribute to substantially improving the database for building a population model. In the end, the realism and precision of the wood mouse model are limited by less informed parameters. To efficiently research literature facing resource limitations (Raimondo et al. 2021), we suggest a reverse approach, i.e. focusing the search for data that inform remaining data gaps when most characteristics are already well informed from multiple sources.

Conceptual model (Phase 3 and Phase 4)

The decision steps in Phase 3 of Pop-GUIDE streamlined and facilitated the derivation of the conceptual model and supported communication with the stakeholder group. In the following, we suggest some improvements, especially for developing conceptual population models for common terrestrial vertebrates and invertebrates.

A decision step, 'Diet preferences', should be added to Pop-GUIDE (Phase 3) that provides guidance on whether and how food preferences should be considered in a model. A dedicated set of questions should be developed that guides through options for inclusion in the conceptual model. Diet preferences can interact with the exposure of individuals because potential food items may differ in residue levels. In addition, animals may adapt their space use according to food availability across heterogeneous landscapes.

We would like to note that the decision step 'diet (indirect effects)' (point 4.1 of Pop-GUIDE, Phase 3) should be clearly separated from the definition of diet preferences. Diet (indirect effects) exclusively addresses potential effects of exposures on food availability of a focal species, e.g. whether pesticide exposures could lead to food limitation. We would recommend addressing indirect effects more generally, i.e. not limited to potential indirect effects due to diet limitation.

Pop-GUIDE should provide guidance for the representation of regular movements. As laid out in the development of the conceptual model for APODEMUS, the interaction with heterogeneous landscapes can lead to different exposures of individuals within and across populations. To account for regular movements in conceptual models, a decision step should be added and linked to the questions about relevant habitat features (point 3.5 of Pop-GUIDE, Phase 3).

Model implementation and evaluation (Phase 5)

A clarification in Pop-GUIDE would be helpful for modellers that 'conceptual model' does not refer to the formalisation of a concept for implementation but to a high-level description of processes in the model, including the clear statement of assumptions.

Comparison of published wood mouse models with APODEMUS

We initiated the development of the APODEMUS model from the ground up. A new model development provided the opportunity to follow a transparent modelling process that complies with best practices and the most current recommendations from regulators on population modelling (Becker et al. 2024) and the European ERA guidance for birds and mammals (European Food Safety Authority 2009, 2023). In addition, it can be tailored to address a specific set of model objectives, whereas the thorough literature review and stakeholder involvement led to a structured and comprehensive derivation of modelling decisions and enabled an evidence-based model development with clear justifications for the processes included in and omitted from the conceptual model.

Nevertheless, APODEMUS includes several similar aspects as in previously published models regarding the representation of general wood mouse ecology and spatial representation. Similarities between models indicate that model objectives led to similar model design decisions. Basing APODEMUS on the extensive literature did not result in major differences in the principal modelling decisions observed in previously published models.

We identified three previously published models representing wood mouse population dynamics and intended for an ERA context. These are a population model by Liu et al. (2013, 2014), the population model POLARIS (Wang et al. 2022) and the food web model Eco-Space (Loos et al. 2010). A comprehensive literature

review has not been reported for any of the three previously published wood mouse models, and the available documentation of the models was limited, particularly for Eco-Space and POLARIS. Only Liu et al.'s model is publicly available.

A major difference of APODEMUS compared to the previous models is the explicit implementation of a physiological model following the DEB theory. Another aspect is the description of habitat attractiveness: previously published models assume and implement a direct influence of vegetation characteristics on wood mouse movement behaviour. However, the literature reviewed did not consistently confirm this interaction with wood mouse movement. Consequently, following Pop-GUIDE, a general approach representing habitat attractiveness was chosen for APODEMUS. Further, for several processes, decisions for APODEMUS deviate in their details from the three previously published models. Short summaries of the three models and how they compare to APODEMUS are provided in the Suppl. material 3.

Discussion

The conceptual model for wood mouse populations in agricultural landscapes (APODEMUS) was developed based on a comprehensive literature review and relevant input from stakeholders. Stakeholder engagement has been crucial in this process, as it allowed extensive discussions and information sharing on wood mouse ecology as well as means to identify and address relevant data gaps. In addition, this type of engagement increased awareness and transparency in the model development process and thereby can facilitate future regulatory evaluations. Furthermore, the process of conceptual model development requires the specification of model capabilities and limitations as well as consideration of the evaluation of the implemented model, which we discuss below. Finally, we provide an outlook of model application for a regulatory pesticide risk assessment.

In the context of pesticide ERA, population models are important contributors to the weight of evidence approach (European Food Safety Authority 2023). Their strengths play out in combining ecological information with information gained in laboratory studies or localised field studies. Exposure and effect predictions become possible for a wide range of risk assessment scenarios (including worst-case scenarios) across geographical regions that otherwise would require long-term, large-scale field exposure experiments. In that sense, population models in ERA provide evidence that would not be accessible otherwise. For a model to be acceptable for application in an ERA, it must be evaluated for its reliability by risk assessors. For APODEMUS, we aimed to facilitate such evaluation with the conceptual model presented in the current paper. We provided the data from the literature (Singer et al. 2025) that were used to inform the model development and followed the systematic stepwise approach of conceptual model development according to Pop-GUIDE (Raimondo et al. 2021). More importantly, we organised a multi-stakeholder workshop which provided a unique opportunity for discussions on wood mouse ecology as well as clear communication on relevant data gaps. At the same time, stakeholders were familiarised with the model development process as well as the wood mouse model concept. This will ultimately facilitate the evaluation process of population models and their application for pesticide ERA.

Transparency regarding the domain of applicability of population models is a prerequisite for their application in risk assessment and to enable their unique ability to estimate potential pesticide impacts under untested conditions. For the wood mouse model, we used publicly available data to develop the concept. In that process, we also identified several data gaps. For example, we identified multiple studies on spatial behaviours in wood mice which supported the implementation of home ranges. However, detailed understanding of movement patterns was lacking, including how individual wood mice make movement decisions in heterogeneous agricultural landscapes. Further, the presence of negative density dependence in wood mouse populations was indicated in multiple publications and is a relatively well-observed phenomenon in small mammal populations, but underlying mechanisms were either not identified or inconsistent among studies. The lack of information about density-dependence mechanisms was in line with a recent review which found that across studies in small mammals, multiple mechanisms were considered potentially important, dependent on context and species (Accolla et al. 2024). Data gaps in model development can be bridged by general theory, extrapolations from related species or simplifying assumptions (Grimm and Railsback 2013). Such decisions included in the conceptual model for APODEMUS were discussed and refined in the stakeholder workshop. Exclusive home ranges of females, as reported in the literature, were discussed as a mechanism for density dependence through a process included in the model. Thus, our conceptual model reflects the available knowledge and achievable certainty on wood mouse ecology.

With the implemented model, analyses will be crucial to address the remaining uncertainties and their consequences for predictions of wood mouse population dynamics. Sensitivity and uncertainty analyses will be used to identify the impact of parameter uncertainties on model outcomes. Parameter values are derived from multiple literature sources and summarise a range of studies, regions and specific measurement methodologies. The range of values from the literature can be applied in model simulations, and the impact on model outcomes can be quantified. Parameters can be identified that have high impacts on model outcomes, such as, e.g. population abundance, demographic structure, spatial distribution and population-level effects. Parameter calibration to available empirical study data provides a pathway to reduce parameter uncertainty. Where parameter uncertainty is impactful but model calibration is not an option (e.g. due to lack of data), parameter value ranges should be considered in model applications. Furthermore, model reliability and accuracy can be demonstrated by comparison of model outputs with empirical population-level observations independent of data used for model development, parameterisation and calibration (Schmolke et al. 2010; Grimm et al. 2014; Railsback and Grimm 2019). For evaluation of spatially-explicit IBMs, a commonly used approach is pattern-oriented modelling (POM) (Wiegand et al. 2003; Grimm et al. 2005; Grimm and Railsback 2012). This method highlights that complex population models should be able to represent multiple aspects of a complex system. We will apply POM to analyse APODEMUS predictions in the context of different field observations. We also expect to calibrate aspects of habitat attractiveness to observed habitat use patterns of wood mice (see “Population and spatial factors”). In addition, the model should be evaluated in the context of different landscapes and climate regions, ensuring the general applicability of APODEMUS across agricultural landscapes in Europe where the wood mouse occurs, rather than specificity to a single region or ERA question.

Finally, it should be noted that APODEMUS was developed to capture variability in wood mouse populations relevant for the objectives of the model, specifically the variability in habitat use within a population occurring in heterogeneous agricultural landscapes. The representation of the wood mouse life cycle means that the age and stage structure of the population varies over time. However, the model does not explicitly address all variability within and across populations occurring in the field. Thus, the model was not developed as a tool to explicitly address the natural variability in wood mouse populations or the normal operating range of the ecological system (EFSA 2016). Rather, APODEMUS was developed to provide reliable relative mean predictions of effects by comparing treatment to control outcomes (as discussed, e.g. by Grimm et al. 2004).

In the current paper, we presented the development of the conceptual model of APODEMUS focused exclusively on the ecology and biology of the species, i.e. without the representation of pesticide exposure and effects. The ultimate aim of the model development is the application of APODEMUS for higher-tier ERAs (EFSA 2023). For this purpose, a sub-model representing organism-level toxic effects (linked to a DEB module) will be integrated in the ecological model. Toxic effects can be derived from laboratory-based studies on surrogate species for each pesticide of interest. Correspondingly, environmental scenarios will contain exposure values across relevant temporal and spatial scales by simulating realistic application rates and the fate of pesticides under evaluation. Dietary uptake of the pesticide will correspond to spatial and temporal overlap of individual simulated mice and environmental concentrations, as the diet composition is currently not explicitly considered in the model. The model including exposures and effects can be applied to scenarios relevant for risk assessments. Examples for such scenarios include landscapes with different levels of compositional and configurational heterogeneity as well as pesticide application regimens and treated crops, also covering different environmental conditions across the geographical range of the species. In addition, scenarios may also address ranges of key model parameters that were identified as influential in the model sensitivity and uncertainty analysis, as well as certain behaviours such as dehusking. Here, a key benefit of modelling is the identification of realistic worst-case scenarios via evaluation of multiple relevant scenarios.

Higher-tier field study data, when available, will be used to calibrate the model to specific local conditions and for validation of exposure–effect assumptions. The final APODEMUS model, calibrated to realistic conditions and validated with field effect data, will then be ready for use in risk assessment with the aim to simulate wood mouse population responses to a wide range of environmental conditions, long-term, including multiple generations, and large-scale. The model is developed for application in support of risk assessment of specific substances. For this purpose, realistic exposures will be simulated and effects quantified on the level of simulated individuals and populations by comparing simulations without (experimental controls) and with pesticide exposure (treatments) at multiple time points. Thereby, population-level properties such as abundance, density and population structure will be the key endpoints evaluated. Finally, the application of exposure multiplication factors in simulations will be used to identify margins of safety and offset any remaining uncertainty in model assumptions (EFSA 2023).

Conclusion and outlook

In the current paper, we presented the conceptual model for APODEMUS as an example of a systematic and transparent model development for use in ERA. In the conceptual model, we made decisions about the model design explicit, addressing processes included in the model and those excluded or simplified for model purposes, as well as discussing the uncertainties that remained. The model development followed best practices as recommended for population models in risk assessments of birds and mammals (European Food Safety Authority (EFSA) et al. 2023).

The conceptual model provides the blueprint for the formalisation of the model for implementation as well as its testing with empirical data (EFSA Panel on Plant Protection Products and their Residues (PPR) 2014; Raimondo et al. 2021). The implemented model will be made publicly available along with its documentation. Open access to the model will further facilitate model evaluation as well as its use.

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Additional information

Conflict of interest

Nika Galic and Amund N. Løvik work for Syngenta; Christian Imholt works for BASF; and Thomas G. Preuss works for Bayer, companies that produce and sell agrochemicals. The work conducted by RIFCON was funded by Syngenta. No funding was provided for participation in the expert workshop.

Ethical statement

No ethical statement was reported.

Use of AI

No use of AI was reported.

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Author contributions

Conceptualization: TG, LI, CI, TGP, ANL, AS, CCM, TM, OJ, JJ, FB, NG, NB, AS. Data curation: CCM, AS, LI, TM, TGP, AS. Formal analysis: TM, AS, AS, TGP. Funding acquisition: LI, OJ. Investigation: MAB, TM, ANL, AS, TGP, AS, SL, CCM. Methodology: OJ, TM, CCM, TGP, SL, AS, MAB, LI, AS. Project administration: OJ, LI, AS, AS. Supervision: LI, SL, AS, OJ, AS. Validation: AS, AS. Visualization: AS, AS. Writing - original draft: AS, AS. Writing - review and editing: CCM, AS, AS, MAB, FB, NB, TG, LI, CI, JJ, OJ, ANL, TM, SL, TGP.

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Data availability

All of the data that support the findings of this study are available in the main text or Supplementary Information.

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Supplementary material 1

Development of a conceptual population model for the wood mouse (*Apodemus sylvaticus*)

Authors: Alexander Singer, Amelie Schmolke, Matthias A. Becher, Felix von Blanckenhagen, Nico van den Brink, Tina Grimm, Lara Ibrahim, Christian Imholt, Jens Jacob, Oliver Jakoby, Silke Laucht, Amund N. Løvik, Thomas Martin, Cynthia C. Muñoz, Thomas G. Preuss, Nika Galic

Data type: pdf

Explanation note: The conceptual model is developed following the Population modeling Guidance, Use, Interpretation, and Development for Ecological Risk Assessment (Pop-GUIDE) (Raimondo et al. 2021). The data informing the model development were compiled from the literature by conducting a comprehensive and systematic review of scientific literature. The step-wise development of the conceptual model is presented. The decision steps follow Pop-GUIDE Phase 3 (Fig. 1) which provides questions organized as dichotomous keys. For each set of questions, we provide a justification for the decisions taken.

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Supplementary material 2

Workshop summary notes

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Data type: pdf

Explanation note: Summary of the stakeholder workshop held to discuss and improve the conceptual model.

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Link: https://doi.org/https://doi.org/10.3897/fmj.7.175714.suppl2

Supplementary material 3

Published population models for the wood mouse

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Data type: pdf

Explanation note: Short summary and review of previously published population models for the wood mouse.

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